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Exploratory behaviour in shrews: fast-lived *Sorex* versus slow-lived *Crocidura*

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Exploration of the environment is a key behaviour in animals. The exploratory behaviour of species or populations depends on different aspects of their ecology. New evidence suggests that differences in exploratory behaviour might also be related to life history strategies, with fast-lived animals (high metabolic rate, short life span) being faster explorers than slow-lived ones. We tested this assumption in shrews. Shrews are divided into two phylogenetic groups, which differ tremendously in life history. We compared the exploratory behaviour of three species, covering both phylogenetic groups. Shrews of the fast-lived genus *Sorex* were quicker to start exploration and to locate the first food patch. They also moved faster than the slow-lived genus *Crocidura*. Unlike many studies on exploratory behaviour that analyse only a short period of time (i.e. a single exploration bout with a fixed duration), we analysed the species-specific allocation of prolonged total exploration time into exploration bouts. Using this method, we could show that *Sorex* performed more, but shorter exploration bouts than *Crocidura*. Our results support the hypothesis of exploratory behaviour being related to life history. While the species we tested occur sympatrically, the two genera differ strongly in the climatic zones they inhabit. It is likely that also during evolution they faced different types of habitat and thus different selection pressures. These differences in evolutionary histories possibly favoured the evolution of their diversified life histories and exploration strategies.

Exploration of the environment is a key behaviour in many animals (Barnett 1958; Hughes 1997; Russell et al. 2009). Generally, animal behaviour is motivated by direct needs: foraging is motivated by the need to feed, courtship by the need to find a mate. In contrast, exploratory behaviour can be conducted without any specific need. During exploration an animal gathers general information about the structural properties of its surroundings and about features such as where to find food (Heinrich 1995) or a possible mate (Schwagmeyer 1995). This information might be helpful later when specific needs prevail. Exploration often occurs simultaneously with other behaviours such as foraging (Winkler & Leisler 1999). This type of exploratory behaviour is defined as extrinsic exploration. In contrast, intrinsic exploration is exploratory behaviour conducted for the sole purpose of gathering information for later use (Glickman & Sroges 1966; Tebbich et al. 2009; reviewed in Hughes 1997).

The exploratory behaviour of species or populations depends on different aspects of their ecology, including diet and habitat characteristics (Greenberg 1990; Mettke-Hofmann et al. 2002; Tebbich et al. 2009). One example is the increased tendency to explore the environment in bird species that feed on concealed food items (Mettke-Hofmann et al. 2002) or that have more diverse diets (Tebbich et al. 2009) compared to species with easily accessible food or less varied diets. Both concealed food and a diverse diet necessitate a higher investment in learning where to find food and consequently more time must be devoted to exploration (Renner 1988). Furthermore, bird species living in complex habitats show higher exploration rates than species living in less complex habitats (Greenberg 1990; Mettke-Hofmann et al. 2002). In complex, variable environments investigation of possible changes via exploration is much more critical to survival than it would be in more simple, stable environments. This would explain higher exploration rates in complex environments than in simple ones.

In the context of behavioural syndromes it has been suggested that the behaviour of individuals or populations is also linked to their life history strategies (Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008). Some studies specifically investigated the relation of exploratory behaviour and basic metabolic rate (BMR; reviewed in Careau et al. 2008, Biro & Stamps 2010). These studies corroborate the expectation that individuals with higher BMRs tend to be more active than individuals with lower BMRs (Mueller & Diamond 2001; Gebczynski & Konarzewski 2009; but see Lantova et al. 2011). Most of the previously mentioned studies focus on differences between individuals (i.e. within a species). However, differences in

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behavioural strategies can also be found between species (Careau et al. 2009; Haupt et al. 2010; Page et al. 2012). Careau et al. (2009) related previously published exploration data of 19 muroid rodent species (Wilson et al. 1976; Webster et al. 1979) to the life history strategies of these species. They found that species with a slow life history (high age of first reproduction and low BMR) spend more time exploring a novel environment than species with a fast life history (low age of first reproduction and high BMR). The authors termed these two strategies as thorough and superficial exploration.

It seems obvious that exploratory behaviour should be related to BMR and life history strategy: animals with higher energetic needs would benefit from the ability to explore novel surroundings and learn about possible sources of food quickly. However, apart from the literature-based rodent study by Careau et al. (2009), we know of no work investigating the relationship between exploratory behaviour and life history using a comparative multispecies approach. To our knowledge, ours is the first study to examine this relationship experimentally.

A promising but until now unexplored model for studying the influence of life history strategy on exploratory behaviour is the family Soricidae (shrews). Belonging to the smallest mammals known, shrews are divided into two phylogenetic groups: red-toothed shrews (Soricinae) and white-toothed shrews (Crocidurinae). Most Soricinae occur in cold and humid climates and are mainly distributed throughout the northern hemisphere. Crocidurinae, in contrast, generally inhabit warm and arid areas, covering the middle and southern part of the Eurasian continent and Africa. In wide parts of Europe (between 36 and 51 degrees of latitude), however, members of the Crocidurinae and Soricinae occur sympatrically and sometimes even syntopically (Churchfield 1990). Both groups mainly feed on insects and other small invertebrates (Churchfield 1990).

Two genera that can be found in the overlapping zone of distribution are *Sorex* (Soricinae) and *Crocidura* (Crocidurinae). While the BMR of shrews of the genus *Crocidura* lies within the typical range for a mammal of this size, shrews of the genus *Sorex* are known for their extraordinarily high BMR (Kleiber 1961; Taylor 1998). To avoid starvation, they must feed every few hours and eat approximately their own body weight per day (Genoud 1988). *Sorex* shrews live just over 1 year. They mostly reproduce after their first winter, but some individuals breed in their first summer (Shchipanov et al. 2005). *Crocidura* shrews, in contrast, live up to 3 years and reproduce for several seasons (Churchfield 1990). Furthermore, *Sorex* has considerably larger litter sizes than *Crocidura* (5.9 versus 3.1 pups/litter; Innes 1994). Considering BMR, life span and litter size, shrews of the genus *Sorex* are a perfect example of animals with a fast-paced life history, whereas *Crocidura* has a much slower life history strategy (Promislow & Harvey 1990).

We investigated whether the differences in life history between *Sorex* and *Crocidura* are reflected in their exploratory behaviour. As experimental species we chose common shrews, *Sorex araneus*, pygmy shrews, *Sorex minutus,* and bicoloured shrews, *Crocidura leucodon*. We analysed their tendency to explore, and manner of exploring, a novel environment in a laboratory experiment. As shrews have a highly diverse diet and will consume most palatable food they encounter while running about, it is not possible to distinguish between exploratory and foraging behaviour. Thus the type of exploration we analysed clearly falls into the category of extrinsic exploration.

We expected the shrews of the fast-lived genus *Sorex* to explore the novel environment faster and more time efficiently, that is covering more space in a shorter amount of time than the slower-lived *C. leucodon*. Based on the findings that rodent species with a slow life history spend more time exploring a novel environment than species with a fast life history (Careau et al. 2009), we further expected *C. leucodon* to explore the novel environment for a longer time than the two *Sorex* species. The BMR of the smaller *S. minutus* is only about 30% higher than that of *S. araneus* (Taylor 1998). We therefore expected, if anything, a slightly faster exploratory behaviour in *S. minutus* than in *S. araneus*.

METHODS

Animals and Housing

In the main experiment, we tested seven *S. araneus* (BMR: 6.1–8.3 ml O2/[g h] (Taylor 1998); mean body mass: 8.4 g, own data), seven *S. minutus* (7.0–12.0 ml O2/[g h]; 4.1 g) and seven *C. leucodon* (2.6 ml O2/[g h]; 9.6 g). In a separate experiment (see Exploration of the Home Terrarium) we additionally tested five *S. araneus*, six *S. minutus* and one *C. leucodon*.

All shrews were caught in Germany either in the area surrounding the Max Planck Institute for Ornithology in Seewiesen or along the river Würm in Gauting, between April 2008 and November 2009. We used wooden box live traps (Mammal Research Institute, Białowieża, Poland), whose 1.4 cm thick wooden walls provide reasonable insulation from warm or cold weather and precipitation. If there was a risk of ground frost we additionally provided cotton wool as bedding. Owing to their rather large size (17 × 8 cm and 10 cm high, 481 g) traps are unlikely to be manipulated or taken by predators; in fact, during trapping sessions we never found that our traps were manipulated or missing. Traps were baited with a few dead mealworms, *Tenebrio molitor*, and a teaspoon of minced beef heart; the amount of food provided was sufficient for a shrew to survive for the short time it would spend in the trap. We checked traps every 2–3 h to minimize the stress and hunger of trapped animals. During the breeding season, we checked the captured individuals upon retrieval from the traps for pregnancy or lactation. Females showing any sign of pregnancy or lactation were released immediately to reduce stress to the pups. As far as is known, shrew pups should not be kept without food for more than about 3 h, the same as for adult shrews of the high-metabolic genus *Sorex* (Churchfield 1990). By checking traps in very short intervals, we gave mothers the opportunity to return to their pups within 3 h. Shrews were transported inside the traps from the place of capture to the keeping facilities; this generally took between 10 and 30 min. Upon completion of our experiments, all shrews were released at the place of capture. Before releasing them, we marked the shrews to avoid multiple testing. Marking was done by bleaching a small patch of fur above the base of the tail with mild, commercially available hair bleach for humans. As we recaptured many marked individuals in the days and weeks after release, we conclude that our marking technique had no adverse short- or long-term effects on shrews. Capturing was conducted with approval from the governmental review board of the Regierung von Oberbayern (licence number: 55.1-8642-8-2007).

Shrews were housed individually, because of their solitary lifestyle (Rychlik 1998), in plastic terraria (44 × 30 cm and 32 cm high) in a climate-controlled room (16–18 °C, 60–70% humidity) at the Max Planck Institute for Ornithology. Terraria were equipped with soil and moss as litter and bowls for water and food. An upturned clay flowerpot filled with hay served as a nestbox. Each shrew was provided with 3 g of live mealworms and 4 g of minced beef heart daily; water was available ad libitum. Shrews were kept on an inverted light:dark schedule (2100 hours light on, 0900 hours light off).

Behavioural observations were conducted in a separate climate-controlled room (same temperature and humidity as the keeping room). The experimental room was evenly illuminated by four infrared LED beams (Tripol, Poland) and presumably appeared dark to the shrews. This presumption is based on the evidently poor